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Distinct Processing of Ambiguous Speech in People with Non-Clinical Auditory Verbal Hallucinations

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Abstract

Auditory verbal hallucinations (hearing voices) are typically associated with psychosis, but a minority of the general population also experience them frequently and without distress. Such ‘non-clinical’ experiences offer a rare and unique opportunity to study hallucinations away from confounding clinical factors, thus allowing for the identification of symptom-specific mechanisms. Recent theories propose that hallucinations result from an imbalance of prior expectation and sensory information, but whether such an imbalance also influences auditory-perceptual processes remains unknown. We examine for the first time the cortical processing of ambiguous speech in people without psychosis who regularly hear voices. Twelve non-clinical voice-hearers and 17 matched controls completed an fMRI scan while passively listening to degraded speech (‘sine-wave’ speech, SWS), that was either potentially intelligible or unintelligible. Voice-hearers reported recognizing the presence of speech in the stimuli before controls, and before being explicitly informed of its intelligibility. Across both groups, intelligible SWS engaged a typical left-lateralized speech processing network. Notably, however, voice-hearers showed stronger intelligibility responses than controls in the dorsal anterior cingulate cortex and in the superior frontal gyrus. This suggests an enhanced involvement of attention and sensorimotor processes, selectively when speech was potentially intelligible. Altogether, these behavioral and neural findings indicate that people with hallucinatory experiences show distinct responses to meaningful auditory stimuli. A greater weighting towards prior knowledge and expectation might cause non-veridical auditory sensations in these individuals, but it might also spontaneously facilitate perceptual processing where such knowledge is required. This has implications for the understanding of hallucinations in clinical and non-clinical populations, and is consistent with current ‘predictive processing’ theories of psychosis.

1 **Introduction**

2
3 Auditory verbal hallucinations (AVH) are typically studied in the context of
4 schizophrenia. However, the presence of other clinical factors, such as additional
5 symptoms or the use of medication, makes it challenging to investigate
6 neurocognitive mechanisms that are hallucination-specific. One solution is to study
7 AVH – or more commonly ‘voice-hearing’ – in the minority of the general population
8 who have such experiences without need for care (Johns *et al.*, 2014). The existence
9 of ‘non-clinical’ voice-hearing has been noted for many years and is strongly argued
10 for by community groups (Romme and Escher, 1989; Corstens *et al.*, 2014).
11 Estimates for voice-hearing in the general population vary from 5% to 15% (Beavan
12 *et al.*, 2011), but rates for frequent and complex voices appear closer to 1–2% (Johns
13 *et al.*, 1998; Kråkvik *et al.*, 2015). Such non-clinical voice-hearing (NCVH) is
14 featurally similar to AVH described in psychosis, but usually more controllable and
15 positive in content (Daalman *et al.*, 2011). Many non-clinical voice-hearers value
16 their experiences and may seek to cultivate them over time (Baumeister *et al.*, 2017;
17 Powers *et al.*, 2017).

18
19 Concerns about stigma make the recruitment of non-clinical voice-hearers extremely
20 challenging: consequently, only a handful of studies have sought to examine the
21 neurocognitive features of NCVH (e.g. Linden *et al.*, 2011; Kompus *et al.*, 2013). The
22 most successful of these was conducted in Utrecht, Holland, which initially identified
23 103 people with frequent NCVH who did not qualify for a psychiatric diagnosis
24 (Sommer *et al.*, 2010). To date, this remains the only project to have managed to run
25 neuroimaging studies in NCVH samples greater than 10 (Diederen *et al.*, 2012; de
26 Weijer *et al.*, 2013; van Lutterveld *et al.*, 2014). These studies have shown that when
27 hearing voices, people with NCVH and clinical AVH engage similar brain networks
28 associated with speech and language processing, including the bilateral superior
29 temporal gyrus (STG), inferior frontal gyrus (IFG) and anterior insula (AI) (Diederen
30 *et al.*, 2012). The experience of NCVH likely also involves regions associated with
31 the generation and monitoring of speech-motor imagery, as well as sensorimotor
32 processes, such as the supplementary and pre-supplementary motor areas (SMA/pre-
33 SMA; Linden *et al.*, 2011; Lima *et al.*, 2016). Atypical modulation of sensory cortex,

1 by attention/monitoring and sensorimotor processes in the SMA/pre-SMA and
2 adjacent anterior cingulate cortex (ACC), has been proposed as a potential mechanism
3 underlying the experience of AVH (Allen *et al.*, 2007).

4
5 In behavioural studies, people with NCVH appear to be particularly susceptible to
6 semantic expectation effects when instructed to monitor for speech in white noise
7 (Daalman *et al.*, 2012), a result similar to effects seen in clinical voice-hearers and
8 members of the general population who report milder, hallucination-like experiences
9 (Ferryhough *et al.*, 2007; Vercammen *et al.*, 2008; Vercammen and Aleman, 2010;
10 Varese *et al.*, 2012). Such effects have been interpreted as evidence of a bias in the
11 perceptual processing of people with NCVH: a prior expectation for linguistic,
12 meaningful percepts that would be sufficient to propagate internally-generated
13 representations (e.g., speech imagery) down through speech and language networks,
14 leading to non-veridical speech perception (Vercammen and Aleman, 2010; Daalman
15 *et al.*, 2012).

16
17 However, if such ‘priors for speech’ are the mechanism underlying NCVH, their
18 influence could be evident not just in speech monitoring tasks but also in speech
19 processing more broadly, particularly when speech perception depends upon prior
20 knowledge to disambiguate a degraded signal. An atypically strong prior for speech
21 could actually facilitate processing, either spontaneously (allowing the hearer to
22 identify potentially meaningful signals more easily) or when specifically directed by
23 instructions (in turn enhancing the discrimination of speech from non-speech). This is
24 consistent with recent evidence reported by Teufel *et al.* (2015) for visual processing
25 in psychosis. People with an “at risk” mental state (i.e., in early stages of psychosis)
26 outperformed controls in their ability to identify objects in ambiguous, Mooney-style
27 visual stimuli (Mooney, 1957), but only once they were given priming information
28 about the objects. That is, people with hallucinations gained more from prior
29 knowledge that could modulate their sensory predictions, leading to better skills in
30 drawing meaning from noise. A similar effect in voice-hearers has never been
31 demonstrated for the auditory domain, but can be tested using an ambiguous auditory
32 stimulus: sine-wave speech.

1 Sine-wave speech (SWS) is a form of acoustically degraded speech, derived by
2 synthesizing tones that track the amplitude and frequency of speech formants (Remez
3 *et al.*, 1981). This can be used to produce potentially intelligible and unintelligible
4 stimuli, based on whether the frequency and amplitude are drawn from the same or
5 different original sentences (Rosen *et al.*, 2011). SWS is typically unintelligible on
6 first exposure and may not be noticed as being speech-like (often sounding like
7 ‘aliens’ or birdsong). Once the listener knows that it is potentially intelligible, though,
8 relatively high levels of comprehension can be achieved (Remez *et al.*, 2011; Rosen *et*
9 *al.*, 2011). Following training, SWS engages a left-lateralized ‘speech mode’ network
10 including anterior and posterior temporal cortex (STG and middle temporal gyrus),
11 IFG and insula (Vouloumanos *et al.*, 2001; Dehaene-Lambertz *et al.*, 2005; Benson *et*
12 *al.*, 2006; Möttönen *et al.*, 2006; McGettigan *et al.*, 2012). Effects of prior knowledge
13 and training on the processing of SWS and similar stimuli are reflected in the greater
14 involvement of inferior frontal cortex (Davis and Johnsrude, 2003), pre-SMA, and
15 dorsolateral prefrontal cortex (Eisner *et al.*, 2010; Rosen *et al.*, 2011), while posterior
16 temporal cortex appears to track changes in sensory detail (Sohoglu *et al.*, 2012) and
17 predictability (Gagnepain *et al.*, 2012).

18
19 Here we used SWS to study whether potential priors for speech in NCVH modulate
20 their spontaneous processing of ambiguous sounds. NCVH participants and matched
21 non-voice-hearing controls passively listened to intelligible and unintelligible SWS
22 while being scanned in fMRI, in a paradigm adapted from a study by
23 Shanmugalingam *et al.* (2012). To disguise the presence of speech, participants were
24 instructed to listen for a target cue (an equivalent noise-vocoded, unintelligible SWS
25 stimulus which sounded ‘noisier’ and ‘rougher’), and were told that the other sounds
26 (intelligible and unintelligible SWS) were ‘distractor’ stimuli (see Fig.1). After 20
27 minutes of scanning (run 1), participants were asked if they had noticed any words or
28 sentences in the distractor stimuli, and if so, when this occurred during the scan
29 (visual markers were displayed during scanning to assist this, e.g., block 1, 2 etc.).
30 Participants were then explicitly told that there was actually speech in some of the
31 stimuli (the ‘reveal’), were trained to understand the SWS sentences within the
32 scanner, and the scan was repeated, with the same set of stimuli and instructions (run
33 2). After scanning, we tested the ability of participants to discriminate between

intelligible SWS and unintelligible SWS (d'), their bias in classifying speech and non-speech (β), and accuracy (number of key words correct).

[Figure 1 here]

We anticipated that voice-hearers would show an enhanced ability to identify intelligible information in SWS when it was present, and our design allowed us to explore when and how this occurred. Behaviorally, if voice-hearers had a pre-existing prior for linguistic percepts, then this could be evident in an earlier recognition point for spontaneously identifying speech in the SWS stimuli. Alternatively, if voice-hearers were more likely to respond to the stimuli as speech-like only when their prior expectation for speech was explicitly modulated (following the reveal and training), this would result in no differences in recognition point, but potentially greater behavioral discrimination of speech and non-speech in the post-scanner task.

Neurally, potentially enhanced predictive representations of speech would be evident in a greater involvement of regions associated with prior knowledge effects on speech perception, including left inferior frontal cortex, pre-SMA and adjacent areas. If this reflected a spontaneous mechanism, then it would be seen before the reveal, and potentially also after; in other words, a general enhancement of the intelligibility response would be evident for NCVH participants. Alternatively, if it required explicit modulation, it would result in an enhancement of the intelligibility response only after the reveal. Both possibilities stand in contrast to the notion that the effect would be driven by differences in low-level auditory processes alone: a low-level effect (contrary to our expectations) would be evident in differential activation of sensory cortical regions (primary auditory cortex, PAC) across groups.

Materials and Methods

Participants

The study included twelve NCVH participants and 17 non-voice-hearing control participants, matched for age, sex, handedness, education, and National Adult

1 Reading Test scores (Nelson, 1982) (see Tab.1). All participants were aware that the
2 study involved voice-hearers, but the project was described as focusing on ‘how the
3 brain processes unusual sounds’, with study materials making no other reference to
4 voices or speech.

5
6 NCVH were recruited in response to an online article for a national newspaper
7 (Alderson-Day, 2014) and via social media, word of mouth, adverts with spiritual
8 organizations, and previous participation in a related project ($n = 4$; the UNIQUE
9 project; see Peters *et al.*, 2016). Participants were included if they were over 18, had
10 never received a psychiatric diagnosis in relation to voice-hearing, and endorsed any
11 of three items derived from the revised Launay-Slade Hallucination Scale (LSHS;
12 Bentall and Slade, 1985; Morrison *et al.*, 2000): *In the past I have had the experience*
13 *of hearing a person’s voice that other people could not hear*, *‘I have heard a voice*
14 *on at least one occasion in the past month*’, or *‘I have been troubled by hearing*
15 *voices in my head*’. Following Sommer *et al.* (2010), a phone screener was used to
16 establish that i) voices were distinct from thoughts and had a ‘hearing quality’, ii)
17 voices were experienced at least once a month, iii) voices were unrelated to drug or
18 alcohol abuse, iv) no psychiatric diagnosis or treatment other than anxiety or
19 depression in remission. Over an 18-month recruitment period, this identified 12
20 individuals who were then interviewed in more detail about their experiences (either
21 at the participant’s home or at a university location) and completed an fMRI scanning
22 session (see Supplementary Materials for interview details). Home visits were
23 necessary due to the large geographical spread of participants across the UK.

24 25 26 ***Stimuli***

27 The SWS stimuli were drawn from a stimulus set developed by Rosen *et al.* (2011)
28 and used in McGettigan, Evans *et al.* (2012). Intelligible (intSWS) and unintelligible
29 SWS (unintSWS) were identical to those previously used apart from being further
30 noise-vocoded (Shannon *et al.*, 1995), a step we deliberately omitted in order to make
31 them less noticeably speech-like. The only exception were the ‘target’ sounds, which
32 were created by noise-vocoding a subset of 10 unintelligible SWS in order to change
33 their timbre and make them distinctive from other stimuli. All SWS stimuli were

derived from Bamford-Kowal-Bench sentences (e.g. ‘The clown had a funny face’; Bench *et al.*, 1979) and recorded by an adult male speaker of standard Southern British English in an anechoic chamber. Frequency and amplitude from the first two formant tracks of each sentence were tracked and modelled with a sine wave tone using a semi-automatic procedure in MATLAB (The Mathworks, Natick, MA). Tracks were reviewed and hand-edited using custom software to ensure accurate tracking (Remez *et al.*, 2011; Rosen *et al.*, 2011). See Supplementary Materials for full details of the SWS preparation methods.

Pre-scan training

All training was conducted without mention of ‘voices’ or ‘speech’. Participants were told that they would be listening to a range of sounds in the scanner, and instructed to listen out for a target sound that would sound ‘different’ or ‘noisier’ than the others. We did not provide information about the potential vocal/speech nature of the stimuli, and did not perform a pre-scan task to assess speech perception abilities, in order to ensure that participants remained naïve regarding our key manipulation, so that spontaneous responses to the stimuli could be examined in the scanner. Participants were played an example target sound three times over Sennheiser HD25 headphones (Sennheiser U.K., High Wycombe, Buckinghamshire, U.K.), and then played three more examples of target sounds along with five non-vocoded unintSWS stimuli, in a random order. Participants indicated with a button-press when they heard a target sound, and the stimulus set was repeated until participants could consistently discriminate targets from non-targets (no participant required the sequence to be repeated more than three times).

fMRI task

Participants listened to the SWS sounds across two identical runs of 20 minutes, broken up into six ‘blocks’ that were marked with a visually presented text stimulus (Block 1, Block 2, *etc.*; see Fig.1). Each run contained 45 intSWS trials, 45 unintSWS trials and 18 target sounds, presented quasi-randomly (one stimulus per trial). Target sounds and 19 silent trials were distributed such that they were presented regularly but unpredictably across the run, with no more than two trials from the same condition

1 occurring sequentially. For each run they were instructed to listen closely for the
2 target sounds and press a button each time one was heard.

3
4 After the first run, while still in the scanner, participants were asked the following
5 questions:

6 1) Did you notice any words or sentences in the sounds you heard?

7 2) If so, do you know when you first noticed them?

8 3) Could you understand the words?

9 4) Could you repeat any of the words?

10 For question 2, participants were asked to estimate when they first noticed that words
11 were present, using the visual markers displayed periodically during the run. This was
12 scored to the nearest block (1–6); for example, if someone reported hearing speech
13 “from the start of block 4 onwards”, they would receive a 4. If participants
14 specifically stated noticing halfway through a block, or were unsure but offered a
15 range (e.g., “some time around block 3 or block 4”), they were allocated a half score
16 (e.g., 3.5, 4.5) in an attempt to be more precise. This score was then used as their
17 individual ‘recognition point’ and treated as a continuous variable for subsequent
18 analyses. Participants were then told that the first run included some potentially
19 intelligible sentences in the non-target stimuli (the reveal), before being played six
20 new intSWS sentences. Participants were played each sentence once, asked to repeat
21 any words they could back to the experimenter, showed a written presentation of the
22 sentence, and then played the sentence two more times, along with the written
23 presentation of the sentence. This combination of distorted auditory presentation and
24 clear written feedback has previously been used to demonstrate effective intelligibility
25 training effects on similar degraded stimuli (Davis *et al.*, 2005). This process was
26 repeated a maximum of twice (for all six sentences) to ensure that participants could
27 decode the potentially intelligible SWS sentences in run 2. The instructions for run 2
28 were the same as run 1, i.e., participants were not instructed to pay attention to the
29 now intelligible SWS sentences and instead to just listen for the target sounds.

30
31 Participants also completed two 5-minute resting-state scans before and after the
32 passive listening run as part of a separate study.

33
34 ***Post-scan behavioral task***

Following scanning, participants were played 50 SWS stimuli in a random order (25 intSWS, 25 unintSWS). For each stimulus, participants told an experimenter i) if speech was present and ii), if so, what was being said. To check that participants could decode new sentences and not just recognize repeated sentences, 20% of the stimuli were new to the participants. Following prior studies, the main outcomes were *keyword accuracy* (number of key words correctly identified in intelligible SWS), d' (sensitivity to speech vs. non-speech), and β (bias in identifying speech as present or absent). The post-scanner task was self-paced and took approximately 15 minutes.

MRI acquisition

MRI scanning was completed on a 1.5T Siemens Avanto (Siemens AG, Erlangen, Germany) using a 32-channel birdcage headcoil. Whole-brain echo-planar images were collected in two runs of 147 volumes each, using a sparse-sampling routine in which auditory stimuli were presented during the silent gap between brain acquisitions (Hall *et al.*, 1999). The following parameters were used: TR = 8.4 s; acquisition time = 3.4s, TE = 0.5s, flip angle = 90°, 40 axial slices, 3mm³ in plane resolution. For localization, high-resolution anatomical images were also acquired using a T1-weighted magnetization prepared rapid acquisition gradient echo sequence (MP-RAGE; TR = 2.73s, TE = 3.57ms, flip angle = 7°, 176 sagittal slices, voxel size = 1mm³).

Auditory onsets occurred 5s (± 0.1 s jitter) before the beginning of the following volume acquisition. The stimuli were presented using Psychtoolbox (Brainard, 1997), running in MATLAB, via a Sony STR-DH510 digital AV control center (Sony, Basingstoke, UK) and MRI-compatible insert earphones (Sensimetrics Corporation, Malden, MA, USA). The sound volume was individually adjusted to a comfortable hearing level prior to scanning. All participants reported being able to hear the sounds without any difficulty.

MRI analysis

MRI analysis was conducted using Statistical Parametric Mapping software (SPM version 8; Wellcome Trust Centre for Neuroimaging, London, UK). The first two volumes of each run were discarded to allow longitudinal magnetization to ensure

1 signal equilibrium. Functional images were realigned with the first volume per run
2 and the anatomical T1 image was then co-registered to the mean functional image.
3 Functional images were then spatially normalized to MNI space using the parameters
4 acquired from segmentation, resampled to 2mm^3 voxels, and smoothed using a
5 Gaussian kernel of 8mm^3 at full-width-half-maximum to ameliorate differences in
6 intersubject localization. Responses for events of interest were modelled using a
7 canonical hemodynamic response function. IntSWS, unintSWS, target sounds and
8 visual stimuli (block titles) were modelled from their onsets with durations of 2
9 seconds, with silent trials acting as an implicit 'rest' baseline. Within each run,
10 individual conditions were modelled as separate regressors in a generalized linear
11 model (GLM), along with six movement parameters derived from realignment (3
12 translations, 3 rotations), that were included as regressors of no interest.

13
14 At the first-level (single-subject), T-contrast images were generated for the
15 comparison of each of the conditions (intSWS, unintSWS, vigilance targets) against
16 the implicit rest baseline. The following planned contrasts were also generated during
17 first-level analyses:

18 i) (intSWS run 1 + intSWS run 2) - (unintSWS run 1 + unintSWS run 2),
19 corresponding to the general effect of intelligibility across runs. If NCVH
20 participants spontaneously responded to intelligible stimuli in a distinct
21 manner, group differences would be expected for this contrast.

22 ii) (intSWS run 2 - unintSWS run 2) - (unintSWS run 1 - intSWS run 1),
23 corresponding to a larger intelligibility response on run 2 vs. run 1, once
24 intelligible SWS were explicitly revealed as speech and participants were
25 trained to understand it. If explicit modulation of expectations was required to
26 trigger a distinct processing of intelligible stimuli in NCVH participants,
27 group differences would be expected for this contrast.

28 iii) intSWS run 1 - unintSWS run 1, corresponding to the intelligibility
29 response prior to the reveal. Finding group differences for this contrast would
30 further support the argument that NCVH spontaneously respond to intelligible
31 stimuli in a distinct manner, and it would establish that the reveal and training
32 are not required for group differences to emerge.

33 iv) intSWS run 2 - unintSWS run 2, corresponding to the intelligibility
34 response post-reveal. Group differences could also be seen for this contrast,

1 but would not directly establish or refute differences in spontaneous
2 processing as participants had already been told about the existence of speech
3 in the intelligible SWS.

4
5 These images were taken up to second-level random effects analyses for group
6 inferences. Where group differences were observed, analyses were repeated
7 controlling for any behavioral differences between the groups (i.e., a difference in
8 recognition point) by including them as covariates in the second-level analyses. We
9 also carried out exploratory individual differences analyses in SPM, to examine
10 associations between neural responses and behavioral performance. All statistical
11 maps were thresholded at $p < .001$ peak-level uncorrected, cluster corrected with a
12 family-wise error (FWE) at $p < .05$ across the whole-brain. All co-ordinates are
13 reported in MNI space. Anatomical labels are based on the SPM Anatomy toolbox
14 (Eickhoff *et al.*, 2005) and the Human Motor Area Template (HMAT; Mayka *et al.*,
15 2006), with images produced using SPM and MRICroGL. Parameter estimates were
16 extracted for plotting using the MarsBaR toolbox (Brett *et al.*, 2002) with ROIs based
17 on the full cluster extent of activated regions in the above analyses. Between-groups
18 comparison of behavioral data was analyzed using two-tailed t-tests at $p < .05$, unless
19 otherwise specified.

22 **Results**

24 ***Behavioral Results***

25 During the training phase, some participants described the sounds as being ‘a bit like
26 a robot’ or ‘like the Clangers’, but no participants described either the target or
27 unintelligible SWS sounds as being speech or voice-like. However, while being
28 scanned, the majority of NCVH participants reported perceiving speech in the SWS
29 stimuli before the mid-scan reveal, with one participant reporting hearing speech from
30 the first ‘three or four words’ of run 1. A significant difference was evident for the
31 recognition point when participants reported first noticing words in the SWS: on
32 average, the NCVH group heard them a block earlier than controls, as shown in
33 Fig.1D (M : 3.71 and 4.94 for NCVH and controls, respectively; $t[27] = -2.17$, $p =$

1 .039¹). Overall, 9/12 NCVH participants (75%) reported realizing that there were
2 words present compared to only 8/17 controls (47%). Of these, seven NCVH and five
3 control participants additionally mentioned that they could understand the words, with
4 five in each group being able to accurately recall some of them.

5
6 During scanning, all participants remained awake and responsive to the target stimuli,
7 as indicated by the button-press data. However, button-press responses for four
8 participants (1 NCVH, 3 controls) did not record correctly and one NCVH participant
9 accidentally pressed a button for every trial. There were no group differences in total
10 button presses, whether or not the latter participant was included (all $t < 1.4$, all $p >$
11 $.19$). Participants with irregular button-press data were marked and checked for their
12 influence on group comparisons of fMRI data (see below). Only one NCVH
13 participant reported a experiencing a hallucination during scanning (a visual
14 hallucination, occurring midway through run 2); however, they did not report this
15 affecting their ability to complete the task.

16
17 On the post-scan behavioral task (i.e., after all participants had been trained to
18 understand the SWS sentences), no differences were observed between the groups,
19 with similar performance for speech discrimination (d'), the ability to comprehend
20 intelligible SWS (keyword accuracy), and bias to classify stimuli as speech (β ; see
21 Supplementary Materials Tab.2).

22 23 ***fMRI Results***

24 *- Responses to intelligible and unintelligible SWS over rest*

25 Compared to rest, responses to intelligible (Fig.2A) and unintelligible (Fig.2B) SWS
26 activated an extensive bilateral fronto-temporo-parietal network, including primary
27 auditory cortex, IFG, SMA, inferior parietal lobule (IPL), and posterior STG. No
28 supra-threshold group differences were evident for either the combination of
29 intelligible and unintelligible SWS vs. rest (i.e., the main effect of group during

¹ Due to non-normal data in the control group this comparison was also run using a permutation test in the *perm* package for R, producing similar results (mean difference = -1.23, $p = .041$, Monte Carlo Method used with 2000 replications).

1 listening to sounds), nor any simple effects (i.e., the main effect of group during
2 listening to intelligible-only SWS vs. rest and unintelligible-only SWS vs. rest).

3
4 [Figure 2 here]
5
6

7 - *Intelligibility effect*

8 Across both runs and groups, several regions were more active for intelligible
9 compared to unintelligible SWS, including the left and right STG, the left middle
10 temporal gyrus, insula, precentral gyrus and IFG, as well as medial regions, namely
11 the pre-SMA, ACC, and medial part of the superior frontal gyrus (Tab. 2a and Figure
12 2c). Between-groups comparisons of the intelligibility response (Intelligible >
13 Unintelligible SWS, planned contrast i) indicated that NCVH participants showed
14 greater activation than controls in a cluster with peaks in rostral ACC, extending to
15 the pre-SMA, middle cingulate cortex, and superior frontal gyrus (Tab.2b and
16 Fig.3C). That is, NCVH showed an enhanced discrimination between intelligible and
17 unintelligible SWS within these regions. Plotting the response of this cluster indicated
18 that the effect was mostly driven by increased responses to intelligible SWS in NCVH
19 (Fig.3C, right panel). To further test this observation, we directly compared the
20 groups' beta values for this cluster within each SWS condition: voice-hearers showed
21 significantly greater responses than controls for intelligible SWS ($t[27] = 2.98$, $p =$
22 $.006$), but the groups were similar for unintelligible SWS ($t[27] = -1.05$, $p = .301$).
23 The reverse contrast (Controls > NCVH) yielded no significant clusters.

24
25 [Figure 3 here]
26

27 As some participants reported hearing speech before the reveal, it could be that group
28 differences evident in the intelligibility response simply reflected NCVH participants
29 having more opportunity to listen to intelligible SWS in 'speech mode'. To examine
30 this, we reran the group comparison of Intelligible > Unintelligible SWS with the
31 timing of participants' noticing of speech – their recognition point – included as a
32 covariate. The group difference in ACC remained significant (MNI coordinates for
33 peak voxel: -2, 32, 26, $k = 467$, $t = 5.27$, $z = 4.31$, $p_{FWE} < .001$), indicating that greater

recruitment of this region by NCVH participants was unlikely to simply reflect a confound resulting from an earlier switch to speech mode. We also confirmed that the pattern of findings remained unchanged when excluding the participant who pressed a button on every trial and those without a full record of button presses; as such, all participants were retained for the remainder of analyses.

- The effect of the reveal: Interaction between run and intelligibility

With the two groups combined, there was a significant interaction for the intelligibility response from run 1 to run 2 in left pSTG (MNI coordinates for peak voxel: -50, -48, 10, $k = 790$, $t = 5.65$, $z = 4.55$, $p_{FWE} < .001$; see Figure 3d). This change was specific to intelligible stimuli, i.e., no effect was evident for the change in responses to unintelligible stimuli (Figure 3d, right panel). This pattern was confirmed in a follow-up analysis, after extracting beta values for this cluster: responses to intelligible SWS were stronger in run 2 than in run 1 ($t[28] = -4.08$, $p < .001$), but responses to unintelligible SWS were similar across runs ($t[28] = 0.12$, $p = .909$).

There were no supra-threshold group differences for an interaction effect from run 1 to run 2 (i.e., planned contrast ii). That is, NCVH participants did not show a specific benefit in intelligibility once trained to listen for speech, indicating that the effect of the reveal and subsequent training had a broadly similar influence on intelligibility responses across groups. Even with a more liberal threshold ($p < .001$ peak level, uncorrected), no clusters over 50 voxels were observed within grey matter.

In the separate analyses for runs 1 and 2 (planned contrasts iii and iv) a clear intelligibility network was observed for run 2 but not run 1 for both groups (see Tab.3), consistent with the non-significant interaction observed. Contrary to what would be expected if group differences were dependent on the explicit modulation of expectation, NCVH already showed a stronger intelligibility response than controls in run 1, in the same ACC region as in the overall analysis (MNI coordinates for peak voxel: 2, 36, 28, $k = 241$, $t = 5.14$, $p_{FWE} = .008$) and in left middle frontal gyrus (MNI coordinates for peak voxel: -36, 54, 0, $k = 190$, $t = 4.91$, $p_{FWE} = .024$). Group differences in ACC for intelligibility were also evident in run 2, albeit at subthreshold levels (MNI coordinates for peak voxel: -4, 38, 20, $k = 51$, $t = 4.12$, $p < .001$

uncorrected), which was consistent with the general enhancement of an intelligibility effect across the whole scanning session.

- Comparing responses in PAC

The lack of supra-threshold group differences in responses to intelligible or unintelligible stimuli over rest indicated that basic auditory processes were broadly similar in controls and NCVH. To explore this further, we extracted average responses to intelligible and unintelligible sounds in the bilateral primary auditory cortices (defined as TE 1.0, 1.1, and 1.2 based on the SPM Anatomy Toolbox) and conducted Bayesian inference testing on effects of group, intelligibility, and run. A Bayesian mixed ANOVA was conducted using JASP (Love *et al.*, 2015), with the default priors (Rouder *et al.*, 2016). When a model containing the group effect was compared to one without it (i.e., the null hypothesis), the Bayes Factor (BF) was 0.54, or 1:1.86 in favour of the null (in other words, the data were almost twice as likely to occur under the null hypothesis). Evidence for any group-related interaction effects was even weaker: BF values of 0.26, 0.26 and 0.57 were observed for models containing group \times run, group \times intelligibility, and group \times run \times intelligibility, respectively (i.e., 1:3.85, 1:3.85 and 1:1.75 in favour of the null)². These values only reflect anecdotal to substantial evidence in favor of the null hypothesis (Jarosz and Wiley, 2014), but they nevertheless offer no evidence at all in favour of potential group differences in PAC signal.

- Individual differences in intelligibility responses

To explore how early responders may have been identifying speech in the SWS, we ran a whole-brain individual differences analysis, including recognition point as a regressor in the Intelligible > Unintelligible SWS contrast. The intelligibility response across runs 1 and 2 in left IFG was negatively related to the recognition point (indicating that those who noticed speech earlier showed greater activation in these regions; see Fig.4a and Tab.4). For run 1 only (i.e., before all participants were in ‘speech mode’), the recognition point was negatively related to responses in the

² BF values for each model were calculated by comparing to the next most complex models lacking those terms (i.e., the three-way interaction model was compared with a model containing all two-way interactions; Rouder *et al.*, 2016).

1 middle cingulate cortex extending to parietal areas (Fig.4b) and positively related to
2 activation in medial prefrontal cortex (Fig.4c). We also ran the same analysis for an
3 index of voice-hearing in the NCVH participants (PSYRATS Physical Characteristics
4 from the past week; see Supplementary Materials); this indicated no significant
5 whole-brain correlations. However, a behavioral correlation was observed between
6 voice-hearing in the past week and recognition point ($r = -.582$, $n = 12$, $p = .047$),
7 such that a greater tendency to hear voices was associated with noticing speech earlier
8 in run 1 (Fig.1D). This correlation directly links auditory-perceptual processes, as
9 evaluated in the current study, with the magnitude of recent AVH.

10
11 [Figure 4 here]
12
13

14 Discussion

15
16 Despite decades of work on hallucinations, little is known about how they relate to
17 everyday perceptual mechanisms. Our research aimed to address this by studying the
18 interaction of expectation and perception in non-clinical voice-hearers. Knowledge
19 and expectations help us to interpret ambiguous signals in a range of contexts; in
20 some cases, this might lead to non-veridical sensations, but in other situations – such
21 as hearing sine-wave speech – such expectations might contribute to divining
22 meaningful signal from apparent noise (Davis and Johnsrude, 2007).

23
24 Behavioral evidence of NCVH hearing semantically congruent (but absent) speech in
25 white noise (Daalman *et al.*, 2012) and signal detection biases in people prone to
26 hallucinations (Brookwell *et al.*, 2013) has been used to argue for the existence of
27 attentional factors – such as expectation and prior knowledge – having a greater
28 influence on perception in people who hear voices. Our design, by initially disguising
29 the presence of speech from participants, allowed us to examine whether such an
30 influence can act spontaneously in NCVH, or requires the specific modulation of
31 expectation (in essence, a suggestibility effect). The subjective behavioral responses
32 of voice-hearers here – reporting the detection of speech content in the acoustics of
33 SWS earlier than controls – suggest a spontaneous tendency in this group to extract

1 meaningful linguistic information from ambiguous signals. Importantly, this finding is
2 complemented by distinct responses seen in brain activity, as indicated by a stronger
3 neural discrimination between intelligible and unintelligible SWS in NCVH. This
4 effect could be seen even before the reveal and training, so was therefore not
5 dependent on the modulation of expectation. Indeed, the comparable levels of
6 discrimination and accuracy in the post-scanner task, and the absence of group
7 differences in how the reveal and training affected brain responses, suggest that the
8 explicit modulation of expectation does not play a major role in how NCVH process
9 ambiguous speech.

10
11 This appears to contrast with the evidence reported by Teufel et al. (2015) that people
12 with hallucinations benefit more from the modulation of prior knowledge, although
13 both findings are potentially consistent with attention and expectation playing a role
14 in unusual perceptions. Under recent ‘predictive processing’ approaches (Clark,
15 2013), perception is understood as the balanced product of expectation-driven
16 predictions (priors) about the external environment, and prediction error signals
17 prompted by new sensory information (Rao and Ballard, 1999; Hohwy, 2014). Most
18 predictive processing models – of hallucination specifically and psychosis more
19 generally – posit a shift towards prior expectations, perhaps as a response to
20 inherently unreliable prediction errors, or a top-down failure to modulate their
21 precision (Grossberg, 2000; Friston, 2005; Fletcher and Frith, 2009; Adams *et al.*,
22 2013; Corlett *et al.*, 2016; Powers *et al.*, 2016). This is not always the case, however:
23 the circular inference model (Jardri and Denève, 2013a), for example, proposes that
24 hallucinations and delusions can result from an over-counting of sensory evidence
25 instead, leading to a confusion of priors and prediction errors (see also Jardri and
26 Denève, 2013b; Leptourgos *et al.*, 2015; Jardri *et al.*, 2016). Had our data only
27 indicated a modulatory effect of the reveal on participants’ responses, then it would
28 have directly supported an enhanced influence of new prior knowledge in the
29 perceptual processing of NCVH (as in Teufel et al., 2015). Instead, the spontaneous
30 orientation towards speech that we observed could either be an indirect indicator of a
31 pre-existing prior for speech, or be explained by differences in how the sensory signal
32 is weighted. We did not observe significant group differences in primary sensory
33 regions (PAC), either in whole-brain analysis or in follow-up Bayesian analysis.
34 However, potential subtle differences in sensory weighting cannot be definitely ruled

1 out using the present design. Further investigation of the intelligibility response using
2 a paradigm that measures prior probability, sensory signal and participant response on
3 a trial-by-trial basis would be required to examine this (for a recent example from
4 decision-making, see Jardri *et al.*, 2017).

5
6 Given the subjective nature of our in-scanner ‘recognition point’ measure, the finding
7 that group differences in the neural responses to SWS were specific to potentially
8 intelligible signals is key. It suggests that NCVH were not simply biased to report
9 perceiving speech in *any* signal, and constrains the discussion of the potential
10 mechanisms driving speech perception in voice-hearers. The lack of differences for
11 any of the separate conditions versus rest, or any differences specific to primary
12 auditory cortical regions, suggests that early auditory processes alone were unlikely to
13 be driving group differences in intelligibility. However, speech areas that are usually
14 associated with effects of prior knowledge and expectation – such as left inferior
15 frontal cortex (e.g. Obleser and Kotz, 2010) – also showed no group differences.
16 Instead, differences were seen in a region of rostral ACC, extending dorsally and
17 caudally to reach the anterior pre-SMA and superior frontal gyrus.

18
19 Although part of the evolutionarily older midline vocalization network (Schulz *et al.*,
20 2005), the ACC is not a classical speech processing area. Nevertheless, ACC
21 responses have been observed for listening to distorted speech (Davis and Johnsrude,
22 2003), and ACC activation correlates with the accurate categorization of phonemes
23 under adverse listening conditions (Du *et al.*, 2014). In hallucinations research, the
24 ACC has been associated with the monitoring and generation of internal and external
25 speech (Simons *et al.*, 2010), and linked to the occurrence of AVH, via atypical
26 modulation of sensory regions (see Allen *et al.*, 2007, for a review). ACC activation
27 has been observed during epochs of spontaneous activity in voice-selective areas of
28 auditory cortex in healthy individuals (Hunter *et al.*, 2006), ‘self-induced’ auditory
29 hallucinations in hypnosis-prone people (Szechtman *et al.*, 1998), and auditory
30 attention in people with sleep-related hallucinations (Lewis-Hanna *et al.*, 2011). ACC
31 involvement was also observed in a number of early symptom-capture studies of
32 people hearing voices while being scanned (e.g., Shergill *et al.*, 2000), although later
33 meta-analyses have failed to consistently identify this region during the hallucinatory
34 state (Jardri *et al.*, 2011; Kühn and Gallinat, 2012; Zmigrod *et al.*, 2016).

1
2 The ACC is associated with a range of processes including attention, error
3 monitoring, affect, and cognitive control (Devinsky *et al.*, 1995). The dorsal,
4 ‘cognitive’ ACC has been proposed to monitor task responses and attention,
5 modulating selection bias and rule application in lateral PFC and inferior frontal
6 cortex respectively (Langner and Eickhoff, 2013). Rostral areas of dorsal ACC appear
7 sensitive to conflicts in response driven by irrelevant stimuli, while more caudal areas
8 manage the allocation of attention (Orr and Weissman, 2009). The extension of this
9 cluster into parts of pre-SMA is also notable given this area’s prior implication in
10 symptom-capture studies of AVH (Linden *et al.*, 2011; Raij and Riekk, 2012),
11 monitoring of inner speech (McGuire *et al.*, 1996), and the generation of sensorimotor
12 predictions that guide and optimize perceptual processes (Lima *et al.*, 2016). The
13 presence of dorsal ACC and pre-SMA together in the voice-hearer response may
14 imply a greater attentional capture and sensorimotor processing of speech-like stimuli.

15
16 The individual difference results also provide clues as to how participants in both
17 groups were able to identify speech in the SWS. Relationships between the
18 recognition point when speech was noticed and activity in left IFG, mPFC, and MCC
19 imply the involvement of both speech-motor processes and amodal, ‘default mode’
20 regions (Raichle *et al.*, 2001). The negative correlation with left IFG activation is
21 consistent with the deployment of this region for parsing speech in adverse listening
22 conditions, and may reflect the accessing of word meanings and segments to support
23 perception via prior knowledge (Davis and Johnsrude, 2003; Obleser and Kotz, 2010;
24 Sohoglu *et al.*, 2012; Du *et al.*, 2014). For instance, Eisner *et al.* (2010) found that the
25 recruitment of the left IFG predicts individual differences in the listeners’ ability to
26 decode vocoded and spectrally shifted speech. Activity in the mPFC, in contrast, is
27 often linked with the default mode network (DMN) and would be consistent with
28 participants taking longer to notice potentially intelligible SWS due to a lack of
29 external engagement (Buckner *et al.*, 2008). The MCC cluster observed here is at the
30 rostral border of the posterior cingulate cortex (PCC) and is sometimes classified as
31 part of the dorsal subdivision of Brodmann Area 23 (e.g. Cauda *et al.*, 2010), which is
32 distinguished from ventral PCC regions posterior to the splenium (Vogt, 2016).
33 Although the PCC and surrounding posterior midline structures are also associated
34 with DMN-like task-negative activity, its dorsal subcomponents have been linked to

1 networks responsible for cognitive control and external attention (Cauda *et al.*, 2010;
2 Leech *et al.*, 2011; Leech and Sharp, 2014).

3
4 Some limitations of the present study must be acknowledged. First, for practical
5 reasons – and because of the goals of the experiment – the behavioural assessment of
6 participants’ ability to discriminate and understand SWS had to be conducted outside
7 the scanner and followed a long period of training and exposure to the stimuli. As
8 such, it is possible that any post-scan group differences were masked or trained out as
9 a result of the procedure, given that decoding of other kinds of degraded auditory
10 stimuli – such as noise-vocoded speech – can improve over time and with training
11 (Davis *et al.*, 2005). However, neither group performed at ceiling on the post-scan
12 task: keyword accuracy after scanning was reasonably low in both groups compared
13 to prior studies using distorted speech (McGettigan *et al.*, 2012), despite the fact that
14 speech/non-speech discrimination was good. In future studies it will be important to
15 assess NCVH participants’ abilities to decode SWS under a variety of listening
16 conditions to measure decoding skill and adaptation more directly.

17
18 Second, we are reliant on the accuracy of participants’ self-reports to gauge when
19 participants noticed speech during run 1, and cannot know for sure what participants
20 were responding to when ‘hearing’ speech. Relying on self-report data is not
21 uncommon in hallucinations research and retrospective reporting of events in the
22 scanner has been used successfully to identify periods of voice-hearing (e.g. Jardri *et al.*, 2013). Nevertheless, it is possible that NCVH participants were just more likely to
23 class any unusual stimuli as speech, rather than intelligible stimuli specifically. Two
24 pieces of evidence militate against such an interpretation, though: first, the lack of any
25 general group differences in the neural response to stimuli versus baseline (i.e., across
26 both intelligible and unintelligible SWS), and second, the lack of any evident speech
27 bias on the post-scan behavioral task. Notably, our brain data provides evidence in
28 favour of a selective effect for the discrimination of intelligible stimuli: an effect that
29 is hard to account by positing a non-specific response bias. Future studies could
30 further address the selectivity of the behavioral effect by testing whether differences
31 in recognition point also exist for a run without potentially intelligible SWS (this
32 would be evidence for a non-specific bias), or by assessing degraded speech
33 perception skills more comprehensively prior to training (e.g., Boebinger *et al.*, 2015).

1 Including such conditions in the current study would have compromised our ability to
2 test naïve participants' spontaneous responses to ambiguous stimuli.

3
4 Finally, we were restricted to a smaller sample of participants in the present study
5 than is generally recommended for clinical fMRI research (Carter *et al.*, 2008) and for
6 group comparisons in general fMRI studies (Poldrack *et al.*, 2017). Recruitment for
7 neuroimaging studies with NCVH groups is extremely challenging: the present
8 sample size is larger than other recent studies (Linden *et al.*, 2011; Kompus *et al.*,
9 2013), with the exception of the Utrecht cohort (e.g. Dideren *et al.*, 2013). Prior
10 NCVH imaging studies have largely confined task-based fMRI investigations to
11 symptom capture (Linden *et al.*, 2011, Dideren *et al.*, 2012) or basic cognitive
12 paradigms, such as dichotic listening (Kompus *et al.*, 2011) or verbal fluency
13 (Dideren *et al.*, 2010), often with recourse to region-of-interest analysis and other
14 methods of constraining analysis (and statistical corrections) to selected brain regions.
15 To our knowledge, this is the first NCVH study to have successfully combined a
16 complex behavioral paradigm with imaging data to examine a potential mechanism
17 underlying hallucination, and while maintaining conservative whole-brain corrections.
18 Nevertheless, small sample sizes in neuroimaging research with clinical and non-
19 clinical voice-hearers is an enduring problem. As we have advocated elsewhere
20 (Alderson-Day *et al.*, 2016) the combination of fMRI data from multiple laboratories
21 provides one means of addressing this issue. The International Consortium of
22 Hallucinations Research (ICHR) is currently supporting ongoing mega-analytic
23 projects involving the combination of task-based, resting-state and structural MRI
24 data from people with AVH (Thomas *et al.*, 2016).

25
26 Notwithstanding the small sample size of the present study, it is also important to note
27 that the general response to intelligibility and general effects of training with SWS –
28 involved regions consistent with previous research on distorted speech. The primarily
29 left-lateralized network seen across both groups is consistent with intelligibility
30 effects using very similar stimuli (McGettigan *et al.*, 2012), as is the involvement of
31 the SMA (Rosen *et al.*, 2011). The involvement of left posterior STG seen
32 specifically following training also replicates prior findings using SWS (Möttönen *et al.*,
33 2006). Thus, in general, these two groups of participants showed plausible
34 responses to the challenge of interpreting SWS.

1
2 In conclusion, the present study represents a first step in the understanding of atypical
3 auditory-perceptual processes in people who regularly hear voices but do not require
4 mental health support. Such individuals do not appear to be differentially affected by
5 explicit modulations of expectation – instead, people in this group report being able to
6 spontaneously extract speech from degraded auditory signals (and report doing so
7 earlier than matched controls). This finding is broadly consistent with predictive
8 processing models of hallucination and perception. The fMRI results indicate that this
9 capacity appears to rely less on enhanced speech-specific feedback to auditory
10 regions, and more on the engagement of sensorimotor and domain-general attentional
11 resources, selectively for potentially intelligible speech stimuli. This suggests that the
12 fundamental mechanisms underlying hallucination involve – and may develop from –
13 ordinary perceptual processes, illustrating the continuity of mundane and unusual
14 experience. It has implications not only for ‘continuum’ views of experiences usually
15 associated with psychosis (Johns and van Os, 2001), but also for the normalization,
16 interpretation, and public understanding of a seriously misunderstood phenomenon.

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24

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32

Supplementary Material

Interview session

The voice phenomenology interview used to assess participants included questions from the Psychotic Symptoms Ratings Scale (PSYRATS; Haddock *et al.*, 1999) and the Positive and Negative Syndrome Scale (PANSS; Kay *et al.*, 1987). To allow for indicative ratings of voice-hearing comparable to AVH, participants were specifically scored on the auditory hallucinations subscale of the PSYRATS and positive and negative subscales of the PANSS (PANSS-P and PANSS-N, respectively). The Beliefs About Voices Questionnaire-Revised (BAVQ-R; Chadwick *et al.*, 2000) was also originally included, although many participants preferred not to complete it because of its focus on malevolent and dominant voices (which they deemed irrelevant to their own experience).

Overall scores on these measures were similar to previous cohorts: positive and negative scores on the PANSS were comparable to those reported by Linden *et al.* (2011) (PANSS-P = 12, PANSS-N = 7), while individual PSYRATS item scores were broadly in line with those reported by Daalman *et al.* (2011) for the Utrecht cohort . The mean score of 4 for P3 (Hallucinations) indicated that participants' voices were rated as 'Moderate' – occurring frequently but not continuously, with thinking and behavior minimally affected (Kay *et al.*, 1987). As would be expected for a voice-hearer group without other psychosis-like characteristics, i) ratings for positive symptoms were significantly higher than negative symptoms ($t[11] = 10.86, p < .001$) and ii) ratings for hallucinations were significantly higher than delusions ($t[11] = 5.86, p < .001$). On average, voices occurred around once a day, for seconds at a time, were located inside the head or close by, and contained very little negative or distressing content. No participants reported that their voices were problematic or disruptive to their everyday lives and all were either in work, education, or retired.

As in some cases a number of weeks passed between the full interview and participants' scanning session ($M(SD) = 77.64 (55.28)$ days), items 1-4 of the PSYRATS (the 'physical characteristics' subscale, assessing frequency, duration, location, and volume of voices) were re-administered via a short phone interview in

the week of the scan. There was no difference observed between scores at interview or in the week of the scan ($t(11) = 1.69, p = .12$). As the most recent index of voice-hearing, this measure was then used for correlation analysis with the behavioural and neuroimaging results from the scanning session.

Supplementary Table 1. PSYRATS item ratings for voice-hearing characteristics, compared with the ‘Utrecht’ sample (Daalman *et al.*, 2011)

	<i>Item</i>	Present Study		Daalman et al. (2011)	
		<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Frequency	1	2.08	1.00	3.53	1.26
Duration	2	1.75	1.14	1.53	0.73
Location	3	2.00	0.85	2.21	1.15
Volume	4	2.00	1.13	1.81	0.65
Beliefs About Voice					
Origin	5	2.25	0.87	3.17	1.13
Emotional Valence	6-8	1.42	1.62	1.69	3.05
Total Distress	9-10	1.66	1.07	0.63	1.33
Control	11	1.17	1.19	1.77	1.49

Note. PSYRATS = Psychotic Symptoms Rating Scale. Individual items are scored from 0-4 by the interviewer. E.g. Frequency: 0 – Voices not present, 1 – Once a week, 2 – Once a day, 3 – Once an hour, 4 – Continuously.

Sine-wave speech stimulus preparation

Potentially intelligible SWS sentences (intSWS) were created by applying the frequency and amplitude estimates of the formants from the same original sentence, while unintelligible SWS control stimuli (unintSWS) combined spectral and amplitude tracks from different sentences (intS_{mod}A_{mod} and S_{mod}A_{mod} respectively in Rosen *et al.*, 2011). For noise-vocoded target sounds, the stimulus waveform was passed through a bank of 16 analysis filters (sixth-order Butterworth) with frequency responses crossing 3 dB down from the passband peak. Envelope extraction at the output of each analysis filter was carried out using full-wave rectification and second-order Butterworth low-pass filtering at 60 Hz. The envelopes were then multiplied by a white noise, and each filtered by a sixth-order Butterworth IIR output filter identical

1 to the analysis filter. The root-mean-square (rms) level from each output filter was set
2 to be equal to the rms level of the original analysis outputs. Finally, the modulated
3 outputs were summed together. The cross-over frequencies for both filter banks (over
4 the frequency range of 70–5000 Hz) were calculated using an equation relating
5 position on the basilar membrane to its best frequency (Greenwood, 1990). Noise-
6 vocoding of the SWS increased the bandwidth of the sinewaves changing their timbre,
7 and excitation with noise ensured that they had a 'noisier/rougher' quality compared to
8 the intelligible and unintelligible SWS stimuli.

9

10 **Supplementary Table 2.** Performance on the post-scan behavioral task

	NCVH		Control		<i>p</i>
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	
Keyword Accuracy	38.33%	14.04%	45.41%	22.72%	0.348
<i>d'</i> (sensitivity)	1.95	0.73	2.02	0.57	0.791
<i>β</i> (bias)	0.68	0.45	0.58	0.85	0.712

11 Note. NCVH = non-clinical voice-hearers.

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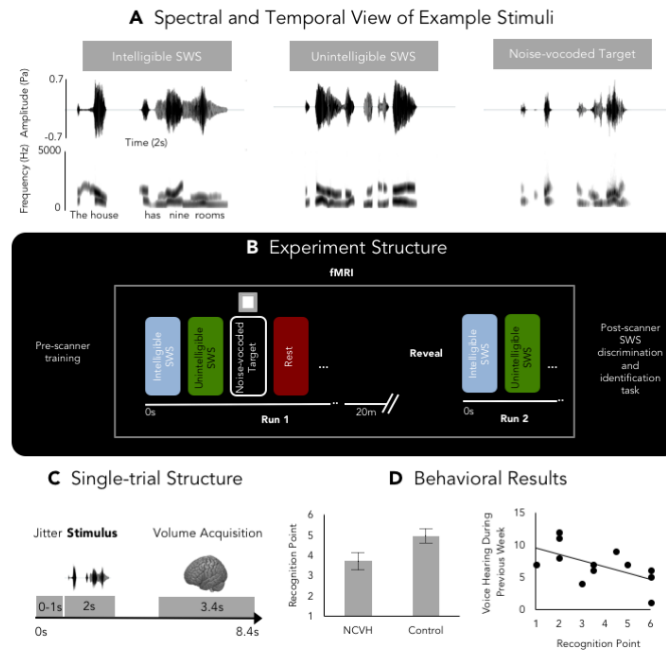


Figure 1. Participants were scanned in fMRI while (A) listening to intelligible SWS, unintelligible SWS, or noise-vocoded, unintelligible target sounds; (B) listening and rest trials were presented in a pseudo-random order across two 20-minute runs, divided by a ‘reveal’ period including training to understand SWS stimuli; (C) each trial lasted 8.4s, including jitter, a 2s stimulus and 3.4s of volume acquisition; (D) NCVH participants recognized speech being present earlier than control participants during run 1 (left panel), and this correlated with voice-hearing during the previous week (PSYRATS – Physical Characteristics subscale). NCVH = non-clinical voice-hearing; PSYRATS = Psychotic Symptoms Rating Scale; SWS = sine-wave speech.

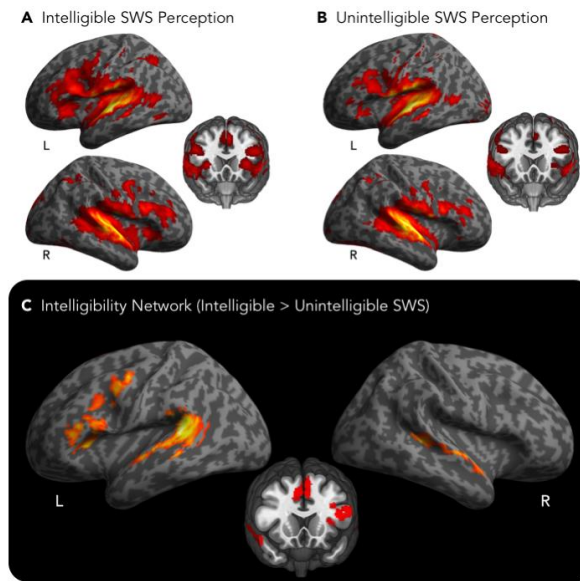


Figure 2. Responses vs. rest baseline to intelligible SWS (A), unintelligible SWS (B), and the difference between them, i.e. the intelligibility effect (C). SWS = sine-wave speech. Activation maps are presented at an uncorrected threshold of $p < .001$ peak level, FWE corrected ($p < .05$) at cluster level.

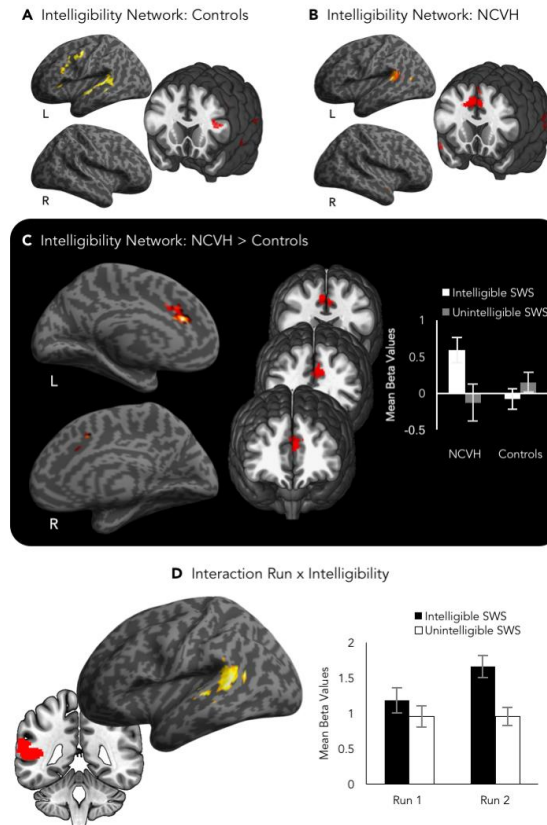
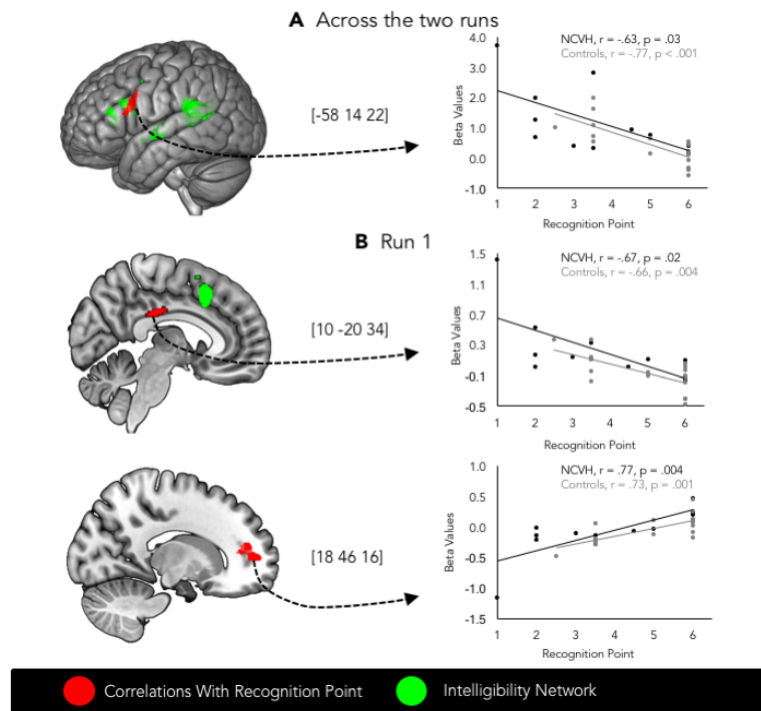


Figure 3. Intelligibility responses in control participants (A), in voice-hearers (B), between-group differences in the intelligibility effect (C), and the change in the intelligibility effect following training with intelligible SWS, both groups combined (D). Beta values shown in (C) are extracted from a cluster with peak in the anterior cingulate cortex (MNI coordinates: -4, 34, 26) identified in whole-brain analysis. Beta values shown in (D) are extracted for a region of left STG (MNI coordinates for peak voxel: -50, -48, 10) identified in the Run \times Intelligibility whole-brain interaction. SWS = sine-wave speech; NCVH = non-clinical voice-hearers. Activation maps are presented at an uncorrected threshold of $p < .001$ peak level, FWE corrected ($p < .05$) at cluster level.

Correlations Between When Participants Noticed Words and Activity in Intelligible > Unintelligible SWS



1

2 **Figure 4.** Correlations between the recognition point when participants noticed words
 3 and intelligibility response across both runs (A), and in run 1 only (B and C). SWS =
 4 sine-wave speech, NCVH = non-clinical voice-hearing. Activation maps are presented
 5 at an uncorrected threshold of $p < .001$ peak level, FWE corrected ($p < .05$) at cluster
 6 level.

7

8

1 **Table 1.** Participant demographic and clinical characteristics

	NCVH		Control		<i>p</i>
Sex	8F/4M		12F/5M		0.822
Handedness	11R/1L		14R/3L		0.474
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	
Age (years)	44.58	14.73	42.47	14.40	0.70
Education (years)	19.08	4.81	18.88	3.12	0.89
NART (max.50)	38.92	3.80	38.47	8.65	0.85
PSYRATS-AH Total	13.17	4.41	-	-	-
PSYRATS-AH 1-4 Interview	7.83	2.66	-	-	-
PSYRATS-AH 1-4 Scanning	6.92	2.97	-	-	-
PANSS-P	13.08	1.98	-	-	-
PANSS-N	8.00	0.95	-	-	-
P1 Delusions	2.33	0.78	-	-	-
P3 Hallucinations	4.00	0.60	-	-	-

2 Note. F = female; M = male; R = right; L = left; NCVH = Non-Clinical Voice-Hearers;
3 NART = National Adult Reading Test; PSYRATS-AH = Psychotic Symptoms Rating Scale -
4 Auditory Hallucinations; PANSS = Positive & Negative Syndrome Scale (P – Positive, N-
5 Negative), P1 and P3 indicate individual PANSS items; higher ratings = greater severity. P
6 values correspond to chi-square tests for categorical data and two-tailed *t* tests (*df* = 27) for
7 continuous data.

8
9

- 1 Table 2. Responses to Intelligible > Unintelligible SWS, across both runs and groups
- 2 combined (A), and group differences in intelligibility responses (B).

Location	x	y	z	# Voxels	t	z	p _{FWE}
A. Runs and groups combined							
L Superior Temporal Gyrus	-62	-42	16	1763	8.24	5.78	< .001
L Superior Temporal Gyrus	-52	-44	20		7.99	5.67	
L Middle Temporal Gyrus	-58	-34	4		6.39	4.95	
L Middle Temporal Gyrus	-58	-16	-2		6.15	4.82	
L Middle Temporal Gyrus	-60	-26	2		5.07	4.21	
L Middle Temporal Gyrus	-56	-62	12		3.58	3.21	
L Middle Temporal Gyrus	-48	-26	0		3.54	3.18	
L Pre-Supplementary Motor Area	-4	16	58	755	6.19	4.84	< .001
R Pre-Supplementary Motor Area	6	18	46		5.58	4.51	
L Pre-Supplementary Motor Area	-4	20	44		4.99	4.16	
R Anterior Cingulate Cortex	8	18	38		4.85	4.08	
L Superior Frontal Gyrus	-6	28	44		4.39	3.78	
L Precentral Gyrus	-48	-2	48	1719	6.07	4.78	< .001
L Inferior Frontal Gyrus	-48	30	14		5.88	4.68	
L Insula Lobe	-32	24	8		5.81	4.64	
L Inferior Frontal Gyrus	-46	16	16		5.34	4.38	
L Precentral Gyrus	-44	2	38		5.33	4.37	
L Inferior Frontal Gyrus	-56	14	22		4.69	3.98	
L Inferior Frontal Gyrus	-40	32	2		4.68	3.97	
L Precentral Gyrus	-42	6	30		4.37	3.77	
L Inferior Frontal Gyrus	-36	14	30		4.26	3.70	
R Superior Temporal Gyrus	62	-6	-4	468	5.71	4.58	< .001
R Superior Temporal Gyrus	60	-16	-2		4.77	4.03	
R Superior Temporal Gyrus	54	14	-14		4.59	3.91	
R Temporal Pole	58	6	-12		4.57	3.90	
R Superior Temporal Gyrus	52	-4	-14		3.72	3.31	
R Superior Temporal Gyrus	48	-36	6	238	5.49	4.46	.001
B. Group differences							
L Anterior Cingulate Cortex	-4	34	26	539	4.81	4.05	< .001
L Middle Cingulate Cortex	-6	16	38		4.61	3.93	
R Pre-Supplementary Motor Area	6	14	42		4.61	3.92	

R Middle Cingulate Cortex	8	22	36	4.40	3.78
L Anterior Cingulate Cortex	0	26	26	4.36	3.76
L Superior Frontal Gyrus	-12	28	32	4.03	3.53
L Superior Frontal Gyrus	-6	30	38	3.84	3.40

1 Note. These results are presented at an uncorrected threshold of $p < .001$ peak level, FWE
2 corrected ($p < .05$) at cluster level. L = Left; R = Right. We report a maximum of 15 grey
3 matter local maxima (that are more than 8 mm apart) per cluster.

4

1 **Table 3.** Intelligibility responses (Intelligible > Unintelligible SWS) separately per
2 run

Contrast	Location	x	y	z	# Voxels	t	z	p _{FWE}
Run 1	-	-	-	-	-	-	-	-
Run 2	L Inferior Parietal Cortex	-68	-42	20	2125	8.96	6.05	< .001
	L Superior Temporal Gyrus	-54	-44	14		8.22	5.77	
	L Middle Temporal Gyrus	-60	-36	6		7.90	5.64	
	L Middle Temporal Gyrus	-60	-26	2		6.55	5.02	
	L Middle Temporal Gyrus	-58	-16	-2		5.47	4.45	
	L Middle Temporal Gyrus	-44	-56	16		5.00	4.17	
	L Middle Temporal Gyrus	-56	-62	14		4.60	3.92	
	L Temporal Pole	-58	8	-12		4.22	3.66	
	L Superior Temporal Gyrus	-60	-2	-6		4.17	3.63	
	L Middle Temporal Gyrus	-40	-64	18		4.13	3.60	
	L Superior Frontal Gyrus	-6	28	44	965	6.49	5.00	< .001
	Pre-Supplementary Motor Area	0	20	46		6.25	4.87	
	L Pre-Supplementary Motor Area	-10	14	56		5.38	4.40	
	L Pre-Supplementary Motor Area	-2	10	60		5.06	4.21	
	R Superior Frontal Gyrus	10	34	44		3.61	3.23	
	L Insula Lobe	-32	24	8	2220	6.37	4.93	< .001
	L Inferior Frontal Gyrus	-46	20	18		5.88	4.68	
	L Inferior Frontal Gyrus	-42	24	0		5.80	4.63	
	L Inferior Frontal Gyrus	-52	12	24		5.68	4.57	
	L Precentral Gyrus	-50	-4	46		5.08	4.22	
	L Inferior Frontal Gyrus	-32	30	-10		5.08	4.22	
	L Inferior Frontal Gyrus	-50	30	8		4.73	4.00	
	R Superior Temporal Gyrus	64	-2	-6	868	6.18	4.84	< .001
	R Middle Temporal Gyrus	56	-36	6		6.04	4.76	
	R Temporal Pole	60	6	-12		5.42	4.42	
	R Temporal Pole	52	4	-14		5.35	4.38	

R Temporal Pole	56	10	-18		5.19	4.28	
R Superior Temporal	60	-16	-2		4.87	4.09	
Gyrus							
R Superior Temporal	44	-38	14		4.83	4.06	
Gyrus							
R Inferior Frontal Gyrus	32	20	-2	216	5.52	4.48	.019
R Inferior Frontal Gyrus	36	32	-6		4.22	3.74	

1 Note. These results are presented at an uncorrected threshold of $p < .001$ peak level,
2 FWE corrected ($p < .05$) at cluster level. L = Left; R = Right. We report a maximum
3 of 15 grey matter local maxima (that are more than 8 mm apart) per cluster.

4
5

Table 4. Relationship between intelligibility responses (Intelligible > Unintelligible SWS) and the point at which participants reported recognizing that speech was present

Run	Location	x	y	z	# Voxels	t	z	p _{FWE}
Run 1 & 2	L Inferior Frontal Gyrus	-58	14	22	189	4.81	4.05	.038
	L Precentral Gyrus	-54	10	30		4.70	3.98	
	L Inferior Frontal Gyrus	-46	30	12		4.46	3.83	
	L Inferior Frontal Gyrus	-52	22	10		3.48	3.13	
Run 1	R Middle Cingulate Cortex	10	-20	34	168	5.00	4.17	.045
	L Middle Cingulate Cortex	-4	-18	32		4.91	4.11	
	R Superior Parietal Lobule	18	-34	34		3.82	3.38	
	L Superior Parietal Lobule	-16	-30	36		3.74	3.32	
	R Superior Frontal Gyrus	18	46	16	167	5.61	4.53	.046
	R Superior Frontal Gyrus	14	52	8		4.81	4.05	
	R Anterior Cingulate Cortex	16	40	10		4.24	3.68	

Note. These results are presented at an uncorrected threshold of $p < .001$ peak level, FWE corrected ($p < .05$) at cluster level. L = Left; R = Right. We report a maximum of 15 grey matter local maxima (that are more than 8 mm apart) per cluster.